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Original article

The Scontrone turtles – A new insular testudinoid fauna from the late Miocene of the Central Mediterranean ☆

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ABSTRACT

We here describe a small turtle assemblage originating from the early Tortonian (late Miocene) palaeoisland of Scontrone, central Italy, a locality previously known mostly for its endemic mammals and giant birds, which were otherwise shared only with the Gargano localities, another fossiliferous area belonging to the same palaeobioprovince. The fossil turtle remains from Scontrone are referred to the geoemydid *Mauremys* sp. and a so far unidentified large-sized testudinid. The biogeographic origins of the Scontrone insular chelonians are discussed. The Scontrone geoemydid adds to the known occurrences of *Mauremys* in the late Miocene of the Mediterranean. The Scontrone large tortoise represents the oldest known Mediterranean insular testudinid, predating significantly the well-known Quaternary endemic island tortoises of the area.

Introduction

Mediterranean islands offer a unique insight into the evolution of several vertebrate lineages and witness the acquisition of extreme and astonishing insular adaptations and species radiations (Van der Geer et al., 2010; Herridge and Lister, 2012; Palombo et al., 2013; Georgalis et al., 2019). Especially for testudinid turtles, Mediterranean islands are long known to have drastically affected the evolution of this lineage, witnessing the radiation and extinction of an array of unique, endemic, and bizarre forms across different insular ecosystems (Leith Adams, 1877; Bate, 1914; Abbazzi et al., 2008; Luján et al., 2017).

Besides the islands that are present today in the Mediterranean Sea, other palaeoislands also existed in the area during its Cenozoic past, that are currently, however, part of mainland Europe (Lanza, 1984). The most prominent and well known among such cases represent the famous fossiliferous localities in Gargano in southern Italy and Scontrone in central Italy, which were during the late Miocene, parts of the Abruzzo-Apulia Platform that has been repeatedly isolated from neighbouring mainland areas for long periods of time (Patacca et al., 2008a, 2008b, 2013). These two localities have been grouped in the same palaeobioprovince, the Apulo-Abruzzi area (Rook et al., 2008). The majority of the different fissures of Gargano pertain to a timespan between the late Miocene and the Pliocene and have yielded a considerably rich fossil fauna over the past decades (Freudenthal, 1971, 1972, 1976, 1985; Ballmann, 1976; Leinders, 1984; Abbazzi et al., 1996; Delfino et al., 2007; Masini et al., 2010, 2013; Masini and Fanfani, 2013; Freudenthal et al., 2013; Villier and Carnevale, 2013; Meijer, 2014; Van Der Geer, 2014; Savorelli and Masini, 2016; Pavia et al., 2017; Pavia, 2013); younger, Early Pleistocene sites, known as Pirro Nord are also known in Gargano (for the reptiles see, among others, Delfino and Bailon, 2000; Blain et al., 2019). Scontrone is older (Tortonian) and has yielded a poorer, though still unique faunal assemblage, comprising also endemic mammals and birds with peculiar morphologies (Rustioni et al., 1992; Mazza and Rustioni, 1996, 2008, 2011; Savorelli et al., 2017; Meijer, 2014; Van Der Geer, 2014; Pavia et al., 2017).

Turtle remains from these unique insular environments of the late Neogene palaeoislands of Gargano and Scontrone have been only poorly known, being solely represented by preliminary descriptions in a thesis of scarce testudinid remains from Gargano (Delfino, 2002) and simple mentions (Mazza and Rustioni, 2008; Patacca et al., 2013; Collareta et al., 2020) or partial descriptions in a thesis (Chesi, 2009b) of *Mauremys* from Scontrone. Here we

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formally describe for the first time all the chelonian remains collected so far (a few specimens are exposed on the rock surface of the site) from the palaeoisland of Scontrone, which document the presence of at least two non-marine turtle lineages. The potential affinities and biogeographic origins of the new turtles from the Scontrone palaeoisland are discussed.

Geological settings

The fossiliferous locality of Scontrone is situated in the Parco Nazionale d'Abruzzo, Lazio e Molise, in Abruzzo region, Central Italy (41°45′15.54″N, 14°02′13.14″E; Fig. 1). The Scontrone fossil site consists of tidal-flat aeolian calcarenites at the base of the *Lithothamnion* Limestone, a Miocene carbonate ramp widespread in the central-southern Apennines (Savorelli et al., 2017). More details about the geology of the locality can be found in Patacca et al. (2008a), Patacca et al. (2013).

The locality is ubiquitously considered to pertain to a palaeoisland. The age of Scontrone is ascribed to the early Tortonian stage of the late Miocene, ca. 9 Ma (Patacca et al., 2013; Savorelli et al., 2017). Associated mammal fauna of Scontrone includes erinaceids, rodents, and hoplitomerycids (Mazza and Rustioni, 1996, 2008, 2011; Savorelli et al., 2007; Van Der Geer, 2014), while giant non-flying birds are also present (Pavia et al. 2017). Among reptiles, only a crocodylian (cf. *Crocodylus* sp.) has been described so far from Scontrone (Delfino and Rossi, 2013).

Fig. 1. The late Miocene (Tortonian) fossiliferous locality in Scontrone, Abruzzo, Italy. **A**. General panoramic view with the site (covered by a sliding protection) in the foreground. **B**. Close up with fossils still embedded in the rock.

Material and methods

All material described herein is permanently curated at the collections of the Centro di Documentazione Paleontologico "*Hoplitomeryx*", Scontrone, Italy. Taxonomy and nomenclature of turtle clades follows Joyce et al. (2020), Joyce et al. (2021).

Institutional abbreviation: SCT, Centro di Documentazione Paleontologico "*Hoplitomeryx*", Scontrone, Italy.

Systematic palaeontology

Testudines Batsch, 1788 [Joyce et al., 2020]
Pan-Testudinoidea Joyce, Parham, and Gauthier, 2004 [Joyce et al., 2021]
Testudinoidea Fitzinger, 1826 [Joyce et al., 2021]
Geoemydidae Theobald, 1868 [Joyce et al., 2021]
Genus ***Mauremys*** Gray, 1869
Mauremys sp.
Figs. 2, 3

Material: SCT 371a (a neural), SCT 371b (two costals and nine shell fragments); SCT 26a (a costal); SCT 26b (a costal); SCT 127a (a fragmentary costal); SCT 43 (five costal fragments and a bridge peripheral); SCT 256 (a peripheral); SCT 285 (a peripheral); SCT 258 (a peripheral); SCT 421 (a peripheral); SCT 416 (a peripheral); SCT 463 (a peripheral); SCT 218 (three peripherals); SCT 422 (a bridge peripheral); SCT 423 (fragment of a bridge peripheral); SCT 140a (a fragmentary ?suprapygal); SCT 233 (right epiplastron); SCT 214b (a left epiplastron); SCT 251 (a right epiplastron); SCT 334 (a right epiplastron fragment); SCT 253 (a fragmentary entoplastron); SCT 301 (a right hyoplastron); SCT 535 (a right hyoplastron on a slab); SCT 249 (a left hyoplastron); SCT 248 (a fragment of hyoplastron or hypoplastron); SCT 339 (a fragment of hyoplastron or hypoplastron); SCT 396 (a fragment of hyoplastron or hypoplastron); SCT 270 (a right hypoplastron); SCT 310 (a partial left hypoplastron); SCT 358 (a fragmentary hyo-hypoplastron); SCT 349 (a right xiphiplastron on a slab); SCT 239 (a left xiphiplastron); SCT 259 (several shell fragments on matrix); SCT 119 (an ilium).

Description

Carapace: The available carapace material consists of a neural, several costals and peripherals, and a probable suprapygal (Fig. 2). The single available neural is SCT 371a (Fig. 2(A)); it is not complete, as its anterolateral edge is broken off, but it is clear that the original general shape was hexagonal, with a concave anterior edge, and posterolateral edges much longer than the anterolateral ones. Most costals are fragmentary (Fig. 2(B, C)). Costal SCT 127a shows the possible trace of a long plastral buttress developed across a few centimetres along its ventral surface. Most shell remains available are peripherals, including bridge ones. SCT 421 is a peripheral pertaining to the beginning or the end of the bridge. Its external surface is characterized by a pleuro-marginal sulcus situated far from the costo-peripheral suture; it bears an intermarginal sulcus. SCT 416 is a complete peripheral originating from the anterior or posterior portion of the carapace, showing a clear intermarginal sulcus, but not a pleuro-marginal one. SCT 463 is a large-sized peripheral (probably peripheral I) that clearly shows the presence of a pleuro-marginal sulcus, as well as an intermarginal one (Fig. 2(F, G)). The peripherals of the bridge are relatively thin if compared with most of the plastral elements. SCT 218 consists of three peripherals of which the central one (which is also the most complete) seems to pertain to the left front of the bridge (Fig. 2(D, E)). It possesses pleuro-marginal and inter-marginal furrows; prior to the beginning of the bridge cavity, at its

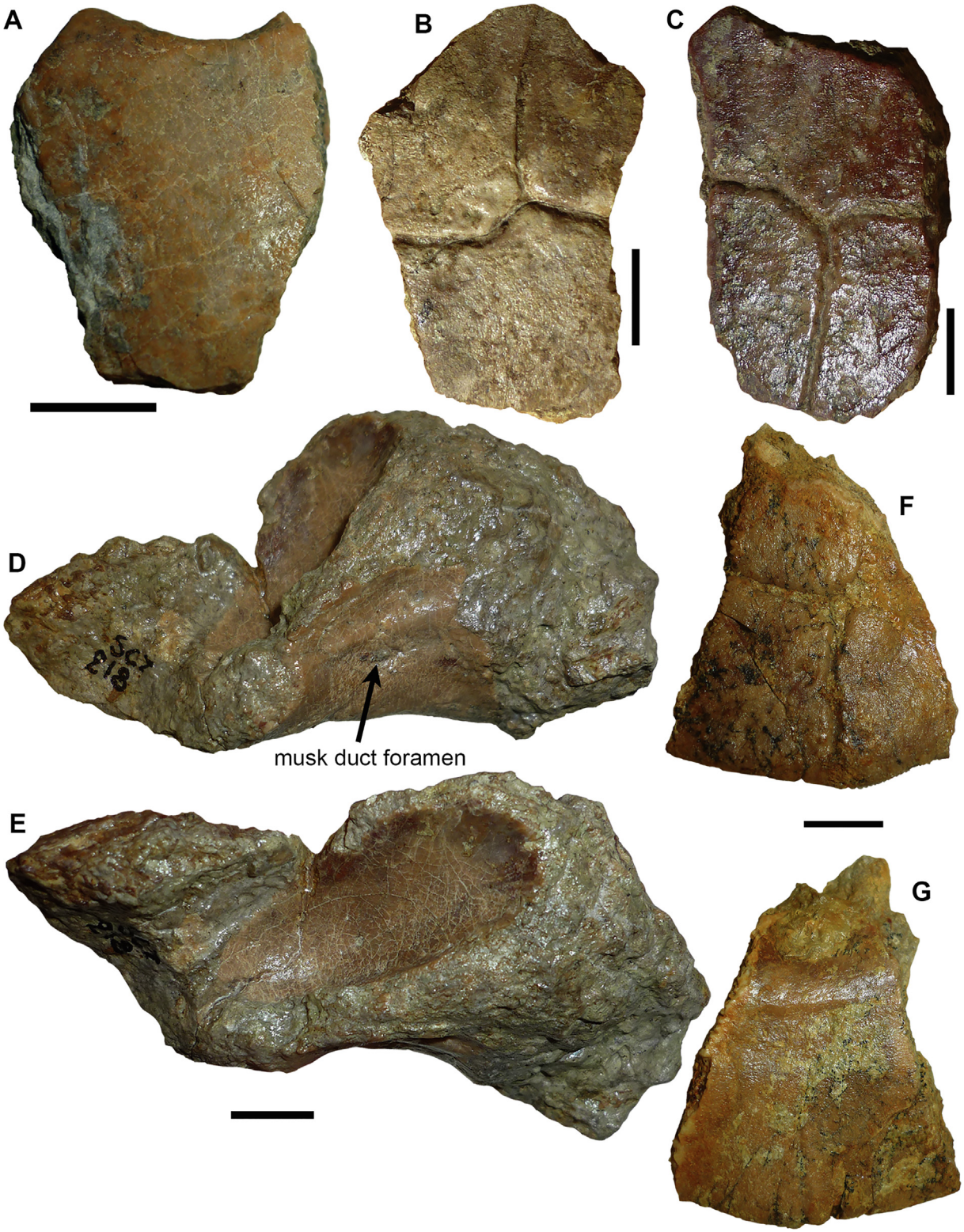

Fig. 2. Carapace elements of *Mauremys* sp. from the late Miocene (Tortonian) of Scontrone, Abruzzo, Italy. **A**. Neural SCT 371a in dorsal view. **B**. Costal SCT 26a in dorsal view. **C**. Costal SCT 26b in dorsal view. **D, E**. Three left bridge peripherals SCT 218 in anteroventral (D) and anterodorsal (E) views. **F, G**. Peripheral SCT 463 in dorsal (F) and ventral (G) views. Scale bars: 10 mm.

ventral surface, there is an elongated depression that could house the musk duct foramen (musk pore). SCT 140a is a fragmentary element that could represent a suprapygal. It is arched in cross-section, with sutures preserved on its ?posterior and ?left sides. A visible longitudinal sulcus is interpreted as the sulcus between the last (likely XII) marginals, whereas a transversal sulcus is interpreted as the sulcus between the last marginals and the fifth vertebral scute.

Plastron: The plastral anatomy is relatively better known than that of the carapace, with plastron represented by epiplastra, an

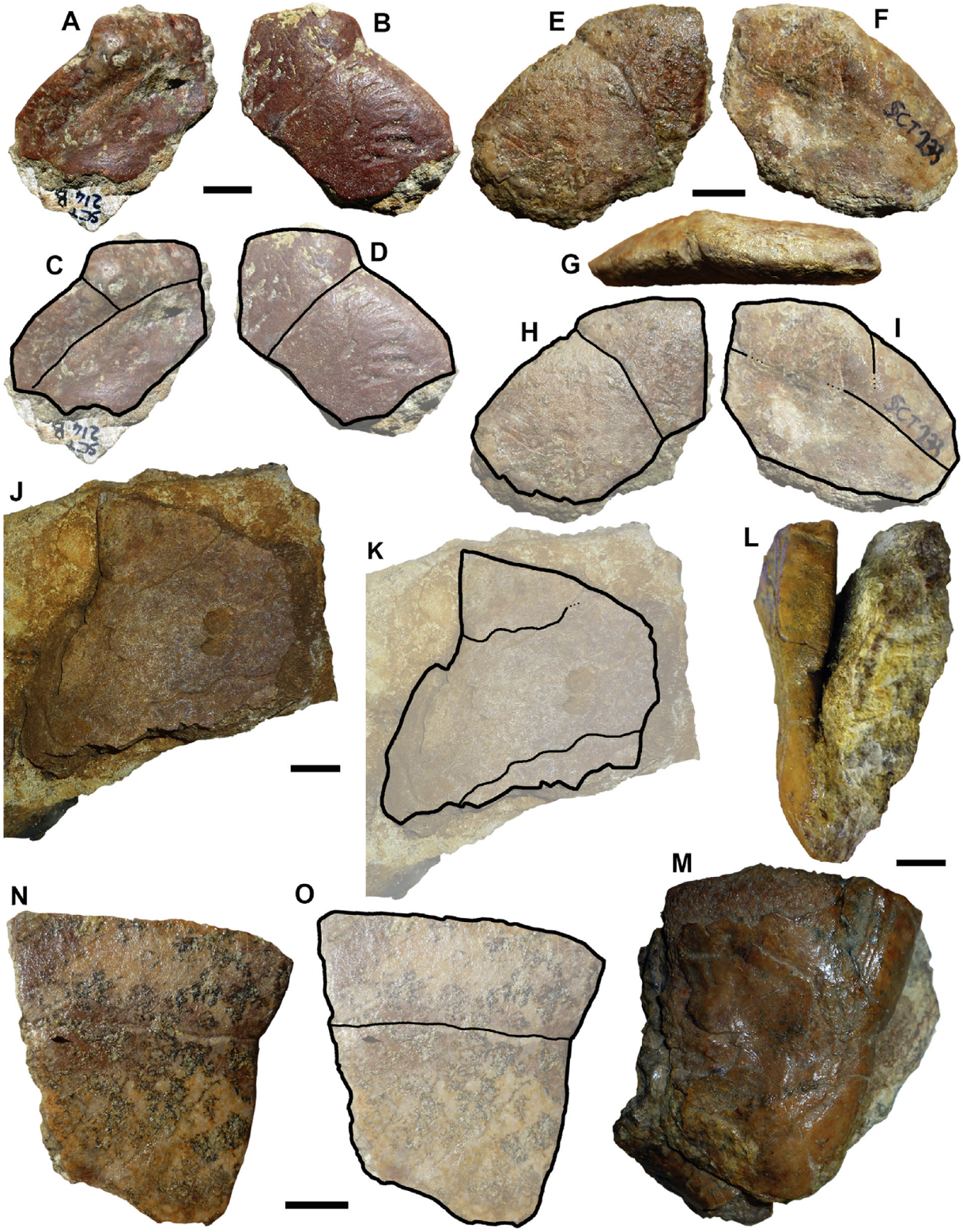

Fig. 3. Plastron of *Mauremys* sp. from the late Miocene (Tortonian) of Scontrone, Abruzzo, Italy. **A–D**. Left epiplastron SCT 214b in dorsal (A), ventral (B), drawing of dorsal (C), and drawing of ventral (D) views. **E–I**. Right epiplastron SCT 233 in ventral (E), dorsal (F), anterior (G), drawing of ventral (H), and drawing of dorsal (I) views. **J, K**. Right hyoplastron SCT 535 on slab (J) and its drawing (K). **L, M**. Right xiphiplastron SCT 349 on slab, in lateral (L) and dorsal (M) views. **N, O**. Left xiphiplastron SCT 239 in ventral (N) and drawing of ventral (O) view. Scale bars: 10 mm.

entoplastron, hyo-hypoplastra, and xiphiplastra (Fig. 3). SCT 214b is a left epiplastron characterized by a slightly developed epiplastral lip (Fig. 3(A–D)). The latter is medially concave (well visible in anterior view). The gularo-humeral sulcus laterally corresponds to a distinct notch on the epiplastron (corresponding also to the lateral edge of the epiplastral lip). The gularo-humeral sulcus intersects the epi-entoplastral suture ca. 7 mm from the interepiplastral suture indicating that the gulars significantly pene-

trated the entoplastron. There is no trace of a gular pocket, but rather only a weak depression posterior to the gular. SCT 251 is an incomplete right epiplastron, with an overall morphology congruent with that of SCT 214b, but slightly larger and thicker, being approximately 46 mm wide (due to erosion, this mediolateral width could be slightly larger in life). SCT 233 and SCT 334 correspond to right epiplastra (Fig. 3(E–I)). SCT 253 is a fragmentary entoplastron. Due to its fragmentary status, it is difficult to assess its exact shape, but it seems that it was wider than long. The sulci visible on the external surface clearly indicate that the gulars covered the anterior tip of the entoplastron and that the pectorals covered its posterior portion (i.e., the humero-pectoral sulcus crosses the entoplastron). On its internal surface there is a clearly elongated xiphoid scar. SCT 301 is a fragmentary right hyoplastron, partly covered by matrix (especially at the sutures with the epiplastron and entoplastron). Its anteroposterior length is ca. 67 mm long, whereas its maximum thickness reaches the 9.7 mm. This specimen preserves the humero-pectoral and pectoro-abdominal sulci. The position of the humero-pectoral sulcus clearly indicates that it crossed the entoplastron quite far from its posterior edge. The humero-pectoral sulcus is anteriorly concave and laterally terminates in correspondence at the weak, but still evident, notch in the lateral side of the anterior lobe of the plastron. The pectoro-abdominal sulcus is anteriorly convex and medially terminates far from the hyo-hypoplastral suture; its lateral termination cannot be evaluated due to preservational reasons. SCT 535 is a right hyoplastron on a slab (Fig. 3(J, K)). The humero-pectoral sulcus is clearly concave anteriorly. The pectoro-abdominal sulcus is equally undulating but is convex anteriorly in the central and middle portions of the hyoplastron, while it forms a deep anterior concavity close to its lateral edge. SCT 249 is a left hyoplastron whose external surface is so damaged that no sulci are visible. SCT 310 is a left hypoplastron that is only partially preserved. On its external surface, the abdomino-femoral forms an anterior convexity close to the lateral edge of the element. SCT 310 is slightly thickened (13.7 mm instead of 9.4 mm) at around its medial suture, in correspondence to the dorsal projection for the bridge buttress. Some further fragmentary elements are partly embedded in matrix but a definite identification cannot be made, such as the possible right hypoplastron SCT 270 and several fragments of hyoplastra or hypoplastra (SCT 248, SCT 339, and SCT 396) that show only their visceral surfaces. SCT 349 is a right xiphiplastron on a slab, situated along with an unidentified bone (Fig. 3(L, M)). This element shows only the visceral surface. Its lateral edge has a modest notch, corresponding to the femoro-anal sulcus, and a deep anal notch. The posterolateral edge of the xiphiplastron is rounded. The structure of the anterior edge of the element indicates the presence of a suture (not of a hinge). The thickness of the xiphiplastron, in the area close to its anterior suture, is 12 mm. SCT 239 is an incomplete left xiphiplastron, missing its anterior portion (Fig. 3(N, O)).

Appendicular skeleton: Only a single appendicular element is preserved, i.e., the ilium SCT 119. The glenoid cavity is not visible, due to preservational reasons, but the area surrounding it is well preserved. The distal (dorsal) edge is poorly preserved but it seems that some residues of concretion are hosted in a lateral, elongated concavity.

Remarks: The overall shape of the preserved skeletal elements along with the probable presence of musk duct foramina is consistent with a referral of the material to Geoemydidae (Claude and Tong, 2004; Garbin et al., 2018; Joyce et al., 2021). Furthermore, the paired marginals XII entering a probable suprapygal, the gulars reaching and overlapping the entoplastron, the humero-pectoral sulcus crossing the entoplastron, as well as the deep anal notch of the xiphiplastra, suggest a referral to the genus *Mauremys* (Hervet, 2000; Claude et al., 2007).

Pan-Testudinidae Joyce, Parham, and Gauthier, 2004 [Joyce et al., 2021]
Testudinidae Gray, 1825 [Joyce et al., 2021]
Testudinidae indet. (large form)
Figs. 4–7

Material: SCT 118 (a partial posterior portion of a plastron partly preserved on a slab); SCT 127b–d (three plastral fragments); SCT 216a (a large shell fragment/unidentified laminar bone); SCT 237 (a ?pectoral girdle on a slab); SCT 163 (a pectoral girdle); SCT 203 (a fragment of a ?pubis); SCT 308 (a humerus); SCT 287 (a fragment of an ilium); SCT 236 (a fragment of a ?humerus); SCT 64 (a caudal vertebra).

Description

Plastron: No carapace material is present and therefore our knowledge on the shell anatomy of this taxon is based exclusively on its plastral remains (Figs. 4, 5). SCT 118 preserves the right hypoplastron and xiphiplastron (Fig. 4). Most of its external surface is covered by sediment but the exposed areas are rugose due to a prominent porosity (in the posterior tip of the xiphiplastron) or an irregular net of fine grooves (in the anterolateral sector of the hypoplastron). On the exposed area there is no evidence of sulci left by the scutes. The internal surface of both elements is relatively smooth. In the hypoplastron, its posterior edge and part of its posterolateral area are characterized by a long and nearly horizontal lateral buttress. The lateral edges of both the hypoplastron and xiphiplastron is not preserved and therefore, the original shape of the lateral edge of the posterior plastral lobe cannot be assessed. The xiphiplastron is nearly complete. This right xiphiplastron is rather thin (3 mm) along its sagittal suture with the (missing) left xiphiplastron but is comparatively much thicker at its posterior end, where a sort of "pad" nearly reaches 30 mm of thickness (the presence of fractures hinders a precise measurement of its thickness). Both the dorsal (visceral) and the ventral (external) surfaces of this posterior "pad" are distinctly convex, but it is not clear whether the ventral convexity reflects the original morphology or whether it is due to preservational reasons. However, this convexity, along with the general structure of the xiphiplastron and that of the hypoplastron, impart to the posterior lobe of the plastron a marked ventral concavity that possibly extended on the anterior lobe as well. The sagittal suture of this right xiphiplastron with its missing left counterpart is ca. 80 mm long; the suture with the hypoplastron is ca. 11 mm long, but it should have been slightly longer as both elements are laterally incomplete. Specimens SCT 127b–d seem also to represent plastral fragments (Fig. 5). None of them shows any sulcus on the external surface. In these plastral fragments, the external surface possesses irregular furrows (as in SCT 118), whereas the internal surface is rather smooth, with the exception of possible vascular sulci.

Appendicular skeleton: SCT 237 is a slab with a fragment of a possible pectoral girdle, preserving the glenoid cavity and the base of both the scapula and acromion (Fig. 6(A)). The rugose area close to the glenoid cavity could represent the contact surface with the coracoid. If so, the acromion is a slightly flattened structure that is a little thicker than the scapula. SCT 163 is a morphologically congruent element with SCT 237, but being isolated, it is more informative (Fig. 6(B)). Both the scapula and the acromion preserve only the area close to the glenoid cavity, which is filled by matrix. The contact surface with the coracoid is located on the ventral half of the acromion, close to the glenoid cavity. This surface is sur-

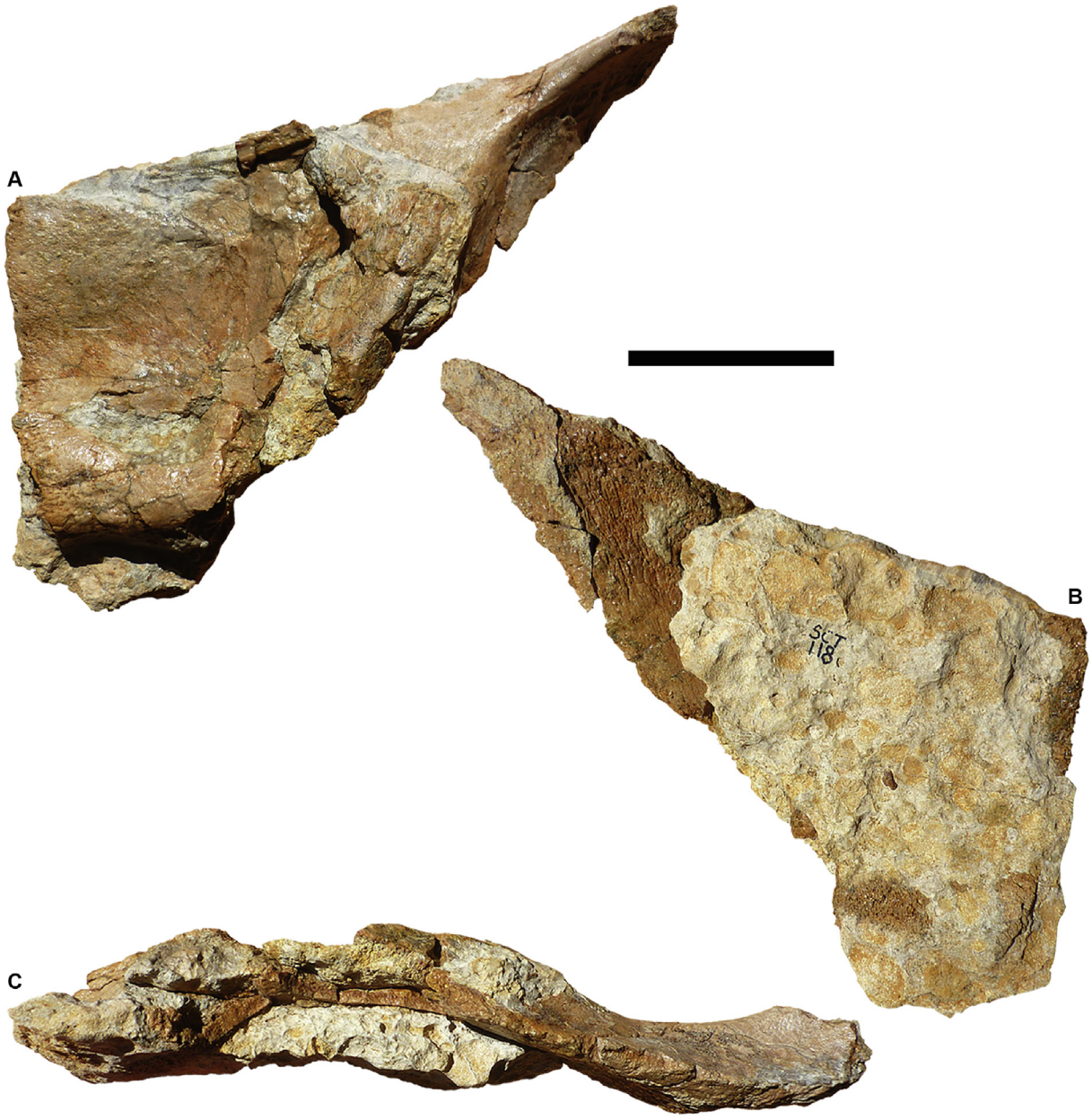

Fig. 4. Plastron of Testudinidae indet. (large form) from the late Miocene (Tortonian) of Scontrone, Abruzzo, Italy. Right hypoplastron and xiphiplastron SCT 118 in dorsal (**A**), ventral (**B**), and posterolateral (**C**) views. Scale bar: 50 mm.

mounted by a distinct tuberosity that is prolonged in a sort of ridge along the dorsal edge of the acromion. Both the scapula and the acromion are flattened and weakly concave on the surface (as the point where the contact surface is), but are slightly convex on the other side. A marked concavity corresponds to the above described tuberosity on the other side of the bone. SCT 203 is a large element that could represent the proximal ramus of a partial pubis (Fig. 6(C, D)). It possesses a triradiate structure with a broad and comparatively thick base distally, thinning into an arched front laterally, which continues into two processes that are broken off. One of the two sides of the thick base is rounded, the other is ridged.

SCT 308 is a fragmentary humerus preserving part of its distal portion, as the distal articulations are missing (Fig. 7(A, B)). The maximum preserved length of the specimen is of 43 mm. The ectepicondylar groove for the radial nerve is well visible. The surface opposite to the groove has, towards the distal epiphysis, a longitudinal modest convexity delimited on both sides by two weak concavities. SCT 236 is a rather fragmentary specimen that could possibly also pertain to a humerus.

SCT 287 could probably represent the dorsal epiphysis of a very stout and large-sized right ilium (Fig. 7(C, D)). The epiphysis itself is not complete and the posterodorsal process is better preserved than the anterior one. The minimum diameters of the preserved portion are 28 and 17 mm, respectively.

Vertebra: SCT 64 is a partially preserved and slightly deformed caudal vertebra (centrum length = 26 mm) (Fig. 7(E, F)). The neural arch is severely damaged, though the elongate and slightly tilted prezygapophyseal facets are still visible. Part of the left postzygapophyseal facet is also present. The left transverse process in approximately horizontal (pointing ventrally only rather slightly) and laterally directed. It is flattened but dorsally provided by a

Fig. 5. Plastron of Testudinidae indet. (large form) from the late Miocene (Tortonian) of Scontrone, Abruzzo, Italy. Plastral fragment SCT 127b in dorsal (**A**) and ventral (**B**) views. Scale bar: 20 mm.

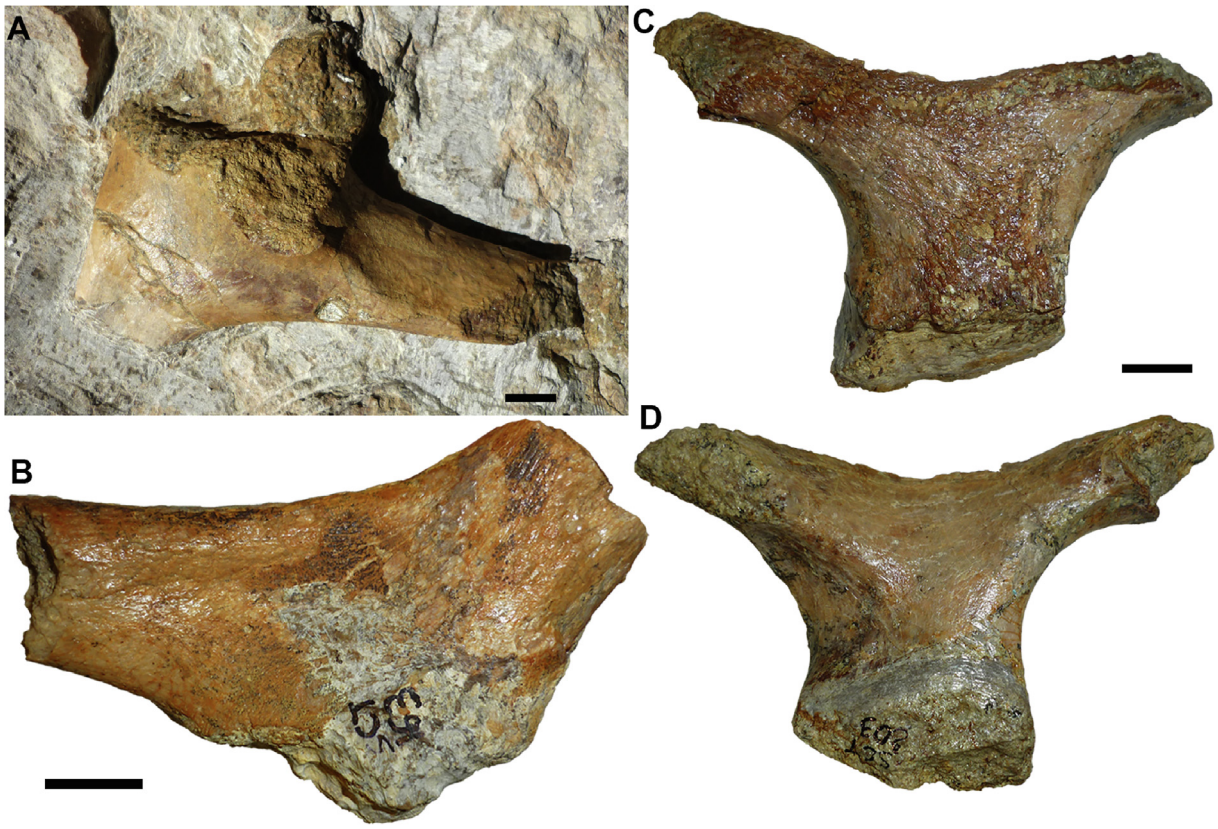

Fig. 6. Appendicular elements of Testudinidae indet. (large form) from the late Miocene of Scontrone, Abruzzo, Italy. **A**. ?Pectoral girdle SCT 237 on a slab. **B**. Pectoral girdle SCT 163. **C, D**. Partial ?pubis SCT 203 in dorsal (C) and ventral (D) views. Scale bars: 10 mm.

modest keel. The neural canal is proportionally small. The vertebra is procoelous and is characterized by two separated articular facets both anteriorly and posteriorly. The cotyle faces anteroventrally, whereas the condyle posterodorsally. The cotylar surfaces are separated by an evident notch. The ventral surface of the centrum is flattened, though a slight longitudinal keel is present at its midline.

Remarks: The presence of developed posterior buttresses on the plastron, along with the general shape of the elements denote a referral to testudinids (Vlachos, 2018). More particularly, within testudinids, the presence of such long and well-developed buttresses in the posterior portion of the plastron would hint for affinities with geochelonans. Within geochelonans, prominent posterior buttresses are characteristic of the

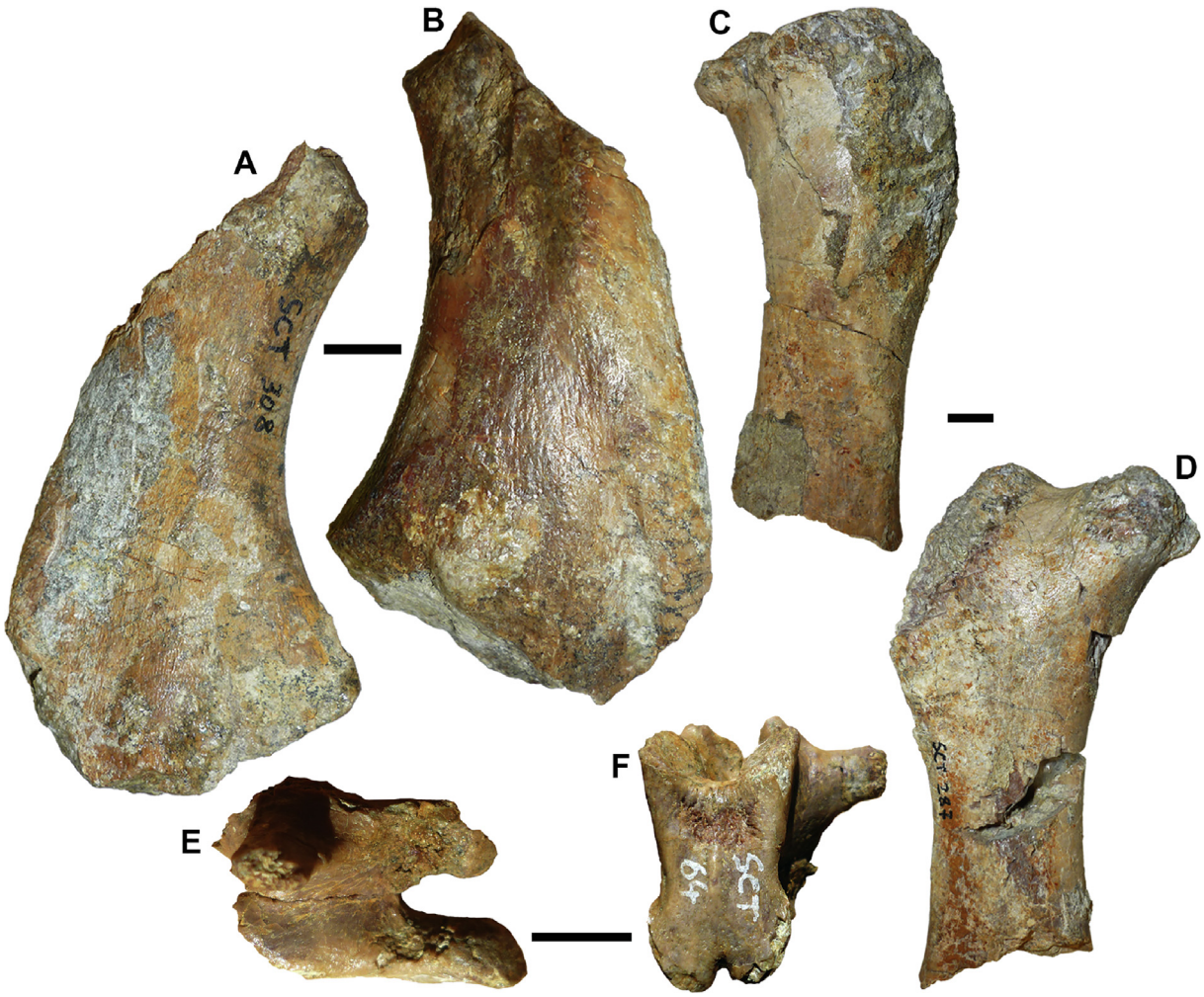

Fig. 7. Appendicular and vertebral elements of Testudinidae indet. (large form) from the late Miocene of Scontrone, Abruzzo, Italy. **A, B**. Partial humerus SCT 308 in posterior (A) and anterior (B) views. **C, D**. Partial right ilium SCT 287 in anterior (C) and posterior (D) views. **E, F**. Caudal vertebra SCT 64 in left lateral (E) and ventral (F) views. Scale bars: 10 mm.

European genus *Titanochelon* Pérez-García and Vlachos, 2014 (Pérez-García and Vlachos, 2014 (Pérez-García and Vlachos, 2014; Vlachos and Rabi, 2018). However, more material is definitely needed in order to conclude whether the Scontrone tortoise has affinities with *Titanochelon* or even with some African form, such as *Centrochelys* Gray, 1872 (which also belongs to geochelonans). In any case, the size of the preserved elements denotes that they pertain to a relatively large form with a relatively short posterior lobe of the plastron, though any estimations about its probable carapace or plastron length would be speculative.

Testudines indet.

Material: SCT 127e–h (four shell fragments), SCT 5, SCT 214c, SCT 214d, SCT 289, SCT 298, SCT 302, SCT 360, SCT 378, SCT 472, SCT 474, SCT 408, SCT 485, SCT 497, SCT 498, SCT 500, SCT 501, SCT 503, SCT 508, SCT 509, SCT 511, SCT 512 (21 shell fragments), and SCT 106, SCT 387, and SCT 394 (three ?shell fragments).

Remarks. Besides the above described specimens, the assemblage comprises also several shell fragments that cannot be more precisely identified. Probably these could also pertain to any of the two testudinoid forms described above, though the presence of an additional taxon cannot be ruled out with certainty. Nevertheless, affinities with trionychids, which are otherwise present in the Tortonian of Italy (Georgalis and Joyce, 2017; Georgalis et al., 2020), can be readily discarded, as the Scontrone shell fragments lack the characteristic sculpturing pattern of that turtle group.

Discussion

The Scontrone palaeoisland

Although not so well known as the nearby Gargano palaeoisland, Scontrone is characterized by an astonishing endemic fauna, comprising, among others, large erinaceids, the peculiar hoplitomerycids, and large non-flying birds (Van Der Geer, 2014; Pavia et al., 2017; Savorelli et al., 2017). Several of these insular taxa have congeneric relatives only in Gargano and nowhere else in the world, such as the iconic large erinaceid *Deinogalerix* Freudenthal, 1972 (Savorelli et al., 2017). Hoplitomerycids are also known exclusively from Gargano and Scontrone: the presence of different but still closely related genera in each palaeoisland, i.e., *Hoplitomeryx* Leinders, 1984, in Gargano, and *Scontromeryx* Van Der Geer, 2014, in Scontrone (Leinders, 1984; Mazza and Rustioni,

1996, 2011; Mazza, 2013; Van Der Geer, 2014) or of a single genus (*Hoplitomeryx*) in both palaeoislands is still debated (Mazza et al., 2016). The large non-flying anseriform bird *Garganornis ballmanni* Meijer, 2014, is also found exclusively in Gargano and Scontrone, notably being represented by conspecific finds in both palaeoislands (Meijer, 2014; Pavia et al., 2017). What appears rather important is the fact that, unlike Gargano that represents a timespan through part of the Neogene, the Scontrone palaeofauna is strictly confined to the early Tortonian, offering thus a definite stratigraphic accuracy and a unique glimpse into insular palaeoenvironments of the Central Mediterranean area of that time.

The origins and exact timing of dispersal of the Scontrone faunal assemblage have been a matter of debate, with different scenarios variously proposed (e.g., Abbazzi et al., 1996; Mazza and Rustioni, 1996, 2008; Masini et al., 2002, 2008, 2013; Rook et al., 2006; Freudenthal and Martín-Suárez, 2010). In general, the whole Abruzzo-Apulia Platform, to which Scontrone belonged, was isolated from Continental Europe at least since the early Oligocene and up to the latest Miocene (Mazza, 2013). In fact, it has been suggested that the last interconnection of the Platform was through a terrestrial land corridor in the Adriatic with northwestern Balkans during the early Oligocene, ca. 29 Ma (Patacca et al., 2008b; Mazza, 2013). It is thus not fully settled whether Gargano and Scontrone were colonized one or multiple times independently, though recent studies have provided strong evidence for the latter case, i.e., multiphasic colonization events (Rook et al., 2006; Savorelli and Masini, 2016; Savorelli et al., 2017). In particular, different scenarios have been proposed for the most famous inhabitants of the Abruzzo-Apulia Platform: for *Deinogalerix* it has been suggested that its origins should be traced in an early to middle Miocene ancestor (Savorelli et al., 2017), whereas for the peculiar hoplitomerycids that they arrived in the area already by the Oligocene (Mazza and Rustioni, 2011).

Palaeobiogeography of the Scontrone turtles

Taking into consideration the complex biogeographic history of the insular Abruzzo-Apulian faunas discussed above, it seems a rather plausible scenario to adhere that the geoemydid and testudinid ancestors of the Scontrone chelonians described herein are of Balkan or even Western Asian origin that arrived in the area during the Oligocene. For *Mauremys*, the possibility of an Oligocene dispersal from the Balkans to Scontrone palaeoisland is hindered by the rather poor and limited fossil record of this genus in the Paleogene of Europe (Hervet, 2004), and particularly in the Balkan Peninsula. In fact, the only Oligocene taxon from the Balkans (but also from the whole Eastern Europe) that could potentially pertain to *Mauremys* is *Mauremys strandi* (Szalai, 1934) from the early Oligocene of Romania (Szalai, 1934; Młynarski and Mészáros, 1963), however, the generic placement of this species is still far from clear. Also, two further Balkan taxa are *Palaeochelys rueckerti* Schleich, 1994, and *Palaeochelys turcica* Schleich, 1994, both from the late Oligocene or early Miocene of the European part of Turkey (Schleich, 1994), however, these are represented by rather incomplete material and their affinities with *Mauremys* are not yet resolved.

On the other hand, African origins have been envisaged for the sole other described reptilian inhabitant of Scontrone, i.e., the crocodylid cf. *Crocodylus*, which has been suggested to represent the product of a direct or indirect marine dispersal from Africa that colonized the palaeoisland of Scontrone during the Tortonian (Delfino and Rossi, 2013).

In any case, fossil record, molecular data, as well as direct observations of extant taxa, attest that *Mauremys* and, especially, large testudinids are well capable of dispersing throughout large marine distances (Gerlach et al., 2006; Vamberger et al., 2014; Kehlmaier et al., 2019; Georgalis et al., 2020). As such, a direct terrestrial corridor would not be strictly necessary for these turtle taxa to reach Scontrone. Therefore, the new geoemydid and large testudinid from Scontrone could represent the product(s) of some dispersal (s) during the late Paleogene and/or Neogene, though we have to leave open the possibility whether such dispersal(s) took place from either Africa, or the Balkans or Central Europe. Nevertheless, in particular for the geoemydid, a Paleogene or early Neogene African origin seems unlikely, as this lineage apparently dispersed to Africa from Europe only during the Tortonian (Georgalis et al., 2020) and is totally absent from pre-Tortonian sediments of Afro-Arabia (Georgalis et al., 2021); therefore, if *Mauremys* reached Scontrone following a southern to northern route, then this would not predate the Tortonian, implying that geoemydids were only new-comers on the palaeoisland, similarly to the case of their crocodylian co-inhabitant (Delfino and Rossi, 2013).

The identification of *Mauremys* in the Scontrone assemblage adds to the known distribution of this genus in Italy, which consists of a ubiquitous faunal element throughout large part of the Neogene and Quaternary, being nevertheless, currently extinct from the area (Sacco, 1889; Portis, 1890, 1896; Kotsakis, 1981; Delfino and Bailon, 2000; Girotti et al., 2003; Chesi et al., 2007, 2009a; Colombero et al., 2017; Collareta et al., 2020; Georgalis et al., 2020). It further attests for a wider distribution of *Mauremys* throughout the Mediterranean during the Tortonian (Georgalis et al., 2016, 2020). As the present material cannot afford an identification to the species level, it cannot be determined whether the Scontrone geoemydid represents an endemic insular form or whether it is conspecific with any of the mainland European taxa, including the Italian extinct species, i.e., the late Miocene *Mauremys campanii* (Ristori, 1891), the Pliocene *Mauremys portisii* (Sacco, 1889), and the Plio-Pleistocene *Mauremys etrusca* (Portis, 1890).

As for the large-sized tortoise from Scontrone, its exact affinities are also hindered by its poor preservational status, which mirrors the one of the few, likewise large, testudinid remains coming from Gargano (Delfino, 2002). Large to giant tortoises were present in Europe throughout most of the Cenozoic (Lapparent de Broin, 2002; Georgalis and Kear, 2013; Pérez-García and Vlachos, 2014; Vlachos et al., 2020). Similarly, large-sized testudinids were also present during the Cenozoic of northern Africa, though their fossil record there is significantly more poorly documented in comparison with their European counterpart (Lapparent de Broin, 2002; Georgalis et al., 2021). In the Mediterranean Islands, testudinids have a relatively rich fossil record, that comprises an array of endemic forms during the late Neogene and Quaternary of several islands (e.g., Malta, Balearic Islands, Sardinia, Sicily), but all of these are from Plio-Pleistocene localities, thus postdating the Tortonian age of the Scontrone material (Leith Adams, 1877; Bate, 1914; Delfino, 2002; Abbazzi et al., 2008; Luján et al., 2017). This diversity and abundance of Mediterranean insular testudinids, strongly evokes the situation in different oceanic islands across the globe. There, several extant and recently (or at least relatively recently) extinct endemic testudinids flourished. These include the famous and diverse radiations in the Galapagos Islands (*Chelonoidis* Fitzinger, 1836; extant), the Mascarenes (*Cylindraspis* Fitzinger, 1836; extinct only few centuries ago), the Seychelles Archipelago and Madagascar (*Aldabrachelys* Loveridge and Williams, 1957; Quaternary, including also an extant taxon), the Caribbean Sea and the Bahamas Archipelago (*Chelonoidis*; Quaternary), and certain more poorly known taxa from the Canary Islands (“*Centrochelys*”; Plio-Pleistocene), the Cape Verde Islands (“*Centrochelys*”; Pleistocene), Indonesia (?*Megalochelys* Falconer and Cautley, 1837; Pleistocene), and Philippines (?*Megalochelys*; Pleistocene) (Günther, 1877; Van Denburgh, 1914; Arnold, 1979; Gerlach, 2004; Setiyabudi, 2009; Rhodin et al., 2015; Vlachos,

2018; Kehlmaier et al., 2019; Georgalis et al., 2021). A principal common feature of almost all of these endemic insular testudinid forms is the acquisition of a large size. These being said, the Scontrone testudinid could be a descendant of any of the late Paleogene or Neogene continental large forms that inhabited Europe and Afro-Arabia, or even of some smaller continental form that eventually evolved a large size during its insular isolation. More remains are definitely needed in order to decipher the exact taxonomic affinities and biogeographic origins of the Scontrone turtles.

We are still only at the beginning of comprehending these unique insular herpetofaunas on these now long-lost islands of the Central Mediterranean. Even though poorly preserved, the Gargano and Scontrone herpetofaunas hint towards interesting dispersal events and unique radiations. It is further evident that Central and Southern Italy played a dynamic role in the biogeography of turtles during the Tortonian, as is also exemplified by recently described coeval finds from Calabria, which could point towards the dispersal of geoemydids and trionychids from Europe to Africa through this part of the Central Mediterranean (Georgalis et al., 2020).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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